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A Problem in the Relation of Temperature to Rate of Insect Development.

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EVEN the most casual observer is familiar with the fact that low temperatures inhibit growth in plants and animals, that hibernation or death will be evidenced by temperatures approaching freezing, and that high temperatures favor rapid development. It is only in late years that biologists have attempted to ascertain with accuracy the reaction of various plants and animals to different degrees of heat. It has now been quite definitely demonstrated that development will take place only when the temperature is above a certain point, called the zero of development, or the threshold of development; that within a certain range of temperatures above this point the increase in the rate of development is approximately proportional to the rise in temperature; and that under given conditions of high moisture, evaporation and other physical environmental factors aside from heat, there is a temperature constant for each period in development, which is equal to the product of the period by the average temperature above the threshold of development.

This range of temperatures within which the rate of development increases as the temperature rises is bounded at the lower end by the threshold of development, and at the upper end by what I shall call the degree of the maximum rate of development. It is found that at temperatures near the lower limit of this range the rate of development varies somewhat faster than the rate of change in temperature, and at temperatures near the upper limit the rate of development varies somewhat more slowly than the rate of change

of temperatures. These facts are of importance to scientists who wish to ascertain the exact relations between temperature and development, but for practical purposes these slight variations need not be taken into consideration, especially when the varying out-of-door temperatures are to be used as a basis of study.

The problem, therefore, dealt with in this paper may be stated as follows: Given the length in days of the period of development at different average daily temperatures, and the average daily temperatures for each of the periods, to find the threshold of development, the degree of the maximum rate of development, the temperature constant, the effects of temperatures above the degree of the maximum rate of development, and how to make corrections in the temperature factor when the temperature for a part of the time during the period was above the degree of the maximum rate of development.

The problem is a simple one when constant temperatures are used, but with widely varying daily temperatures as a base for study the problem is more difficult, since the average daily temperatures for the periods must be used and in nearly all observations these are influenced by temperatures below the threshold of development or temperatures above the degree of the maximum rate of development.

In this paper the method of procedure will be illustrated by studies on the pupal period of the *Carpocapsa pomonella,* based on observations out of doors on the pupal period of 3,817 pupæ at mean daily temperatures varying from 52.6° F. to 82.6° F.

The following table gives the complete results of the study:

RELATION OF TEMPERATURE TO LENGTH OF PUPAL PERIOD.

Temperature range.	Generation.	Number of observations.	Harmonic average of period.	$\frac{1}{P}$	Average mean daily temperature.	Average daily day-degrees.			Total day-degrees.	
						52+	2(87+)	(52+)—2(87+)	52+	(52+)—2(87+)
52–55....	Hib.....	2	45.5	.021	52.6	5.1	.....	5.1	236	236
54–55....	Hib.....	348	35.2	.028	55.7	6.8	.....	6.8	237	237
56–57....	Hib.....	976	34.0	.029	56.1	7.0	.....	7.0	240	240
58–59....	Hib.....	243	27.7	.036	58.5	8.6	.....	8.6	241	241
68–69....	First and second,	218	13.8	.072	69.2	17.3	.....	17.3	238	238
70–71....	First and second,	175	12.7	.078	70.7	18.7	.04	18.7—	238	238
72–73....	First and second,	221	11.5	.086	73.1	21.1	.24	20.8	242	240
74–75....	First and second,	247	10.7	.093	74.9	22.9	.42	22.5	245	241
76–77....	First and second,	517	10.0	.099	76.7	24.7	.88	23.8	248	239
78–79....	First.....	481	9.4	.105	79.1	27.1	1.63	25.5	256	240
80–81....	First.....	133	9.4	.106	80.8	28.8	3.52	25.3	272	239
82–83....	First.....	256	9.2	.108	82.6	30.6	4.12	26.5	283	245
52–83....	.....	3,817	14.4	.669	.....	17.3	.77	16.6	251	240

The usual method for determining the threshold of development is to use the reciprocals of the periods and the average mean daily temperatures as the coördinates and plot the one against the other, then draw a line which best fits the points, and the point where it crosses the temperature axis is the threshold of development. This method serves quite well when the temperatures are constant, but the more widely the temperature varies during the daily variations the less accurate are the results. The accompanying figure is really four figures placed on the same sheet, and represents the points in the various positions assumed by them at the different stages in the solution of the problem.

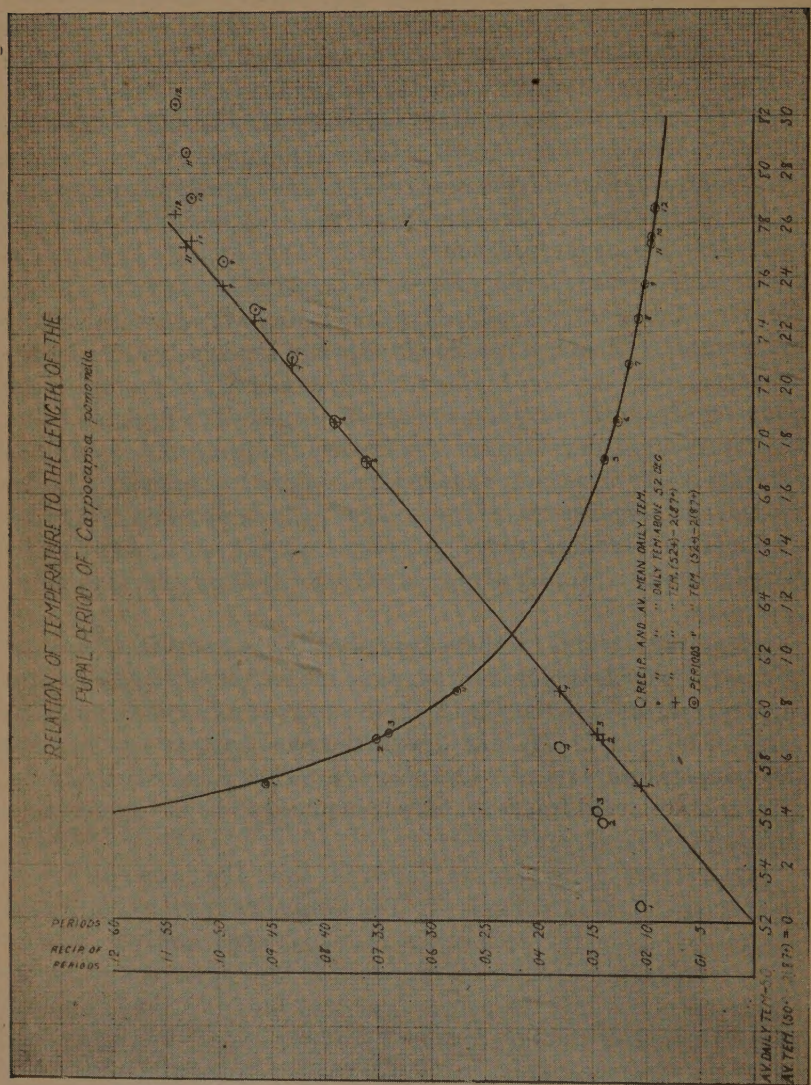
The circles represent the position of points resulting from plotting the reciprocals of the periods against the average mean daily temperatures. These points do not fall in a straight line, but at the lower end they are too far to the left, because the average mean daily temperatures are the averages of temperature readings below the threshold of development (ineffective temperatures) as well as readings above this point, and the points at the upper end are too far to the right, because the average mean daily temperatures here are averages of readings above the degree of the maximum rate of development (retarding temperatures) as well as readings below this point.

A line that would fit these points would be too flat. Now the points that are least affected by these ineffective and these retarding temperatures are those between the average mean daily temperatures of 68 and 72. A line drawn through these two points cuts the temperature axis at 51.92 degrees. This is so nearly 52 degress that, to avoid fractions, 52 was assumed to be the approximate threshold of development.

The average daily degrees above 52 were then computed with results as shown in column 7. The points marked by dots were plotted by using the reciprocals of the periods and the average daily temperatures above 52 degrees. It will be seen that at the lower end of the line the points come into line with the two points used to establish the line, but at the upper end of the figure they are in the same position as the points located by plotting reciprocals against average mean daily temperatures.

It was necessary now to ascertain the degree of the maximum rate of development. The only way to determine this point is by trial.

It was assumed at first that temperatures above the degree of the maximum rate of development were ineffective and did not ac-


RELATION OF TEMPERATURE TO THE LENGTH OF THE
PUPAL PERIOD OF Carpocapsa pomonella
PERIODS
RECIP. OF PERIODS
AV. DAILY TEM.
AV. TEM. (30° = 0)
C RECIP. AND AV. MEAN DAILY TEM.
• " " " DAILY TEM. ABOVE 52.26
+ " " " TEM. (52.26) - 2(87°)
⊙ PERIODS " " TEM. (52.26 - 2(87°))

celerate the rate of development. On this supposition 84, 85, 86, 87, 88 and 89 were taken in turn as the degree of the maximum rate of development and the proper corrections made. This did not bring the points back into line, as the points higher up still stood too far to the right. It was then assumed, after a careful inspection of the data, that temperatures above the degree of the maximum rate of development not only did not accelerate but retarded the rate of development in the same proportion as an equal fall in temperatures below this point would retard it.

On this supposition 84, 85, 86, 87, 88 and 89 degrees were in turn taken as the degree of the maximum rate of development, and corrections made in the location of the points in each case. It was found that 87 degrees gave the best results. Points represented by the crosses were then plotted, using the reciprocals of the periods and the average daily temperatures above 52 degrees, diminished by twice the average daily temperatures above 87 degrees. This brought all the points nearly in line with the two original points used in determining the line, indicating that the second supposition relative to the effects of temperatures above the degree of the maximum rate of development is correct and that 87 degrees is approximately the degree of the maximum rate of development.

The corrections for temperatures above 87 degrees are entered in column 8 and the corrected average effective temperatures (day-degrees) are entered in column 9.

The day-degree is used as the thermal unit and is equivalent to a temperature of one degree lasting for one day. The product of the day-degrees above 52 degrees (column 7) by the periods (column 4) are entered in column 10. It will be noted that they are nearly constant for the lower temperature, but increase as the higher temperatures are reached.

The product of the day-degrees above 52 degrees diminished by twice the day-degrees above 87 degrees (column 9) are recorded in column 11. It will be seen that they are nearly constant for all temperatures.

The average of these products is 240.

The formula is $C = P(T - 2t')$ in which $C =$ constant. $P =$ period in days, $T =$ average day-degrees above 52 degrees and $t =$ average day-degrees above 87 degrees. This formula is the equation of an hyperbola. Plotting the periods expressed in days against the effective day-degrees $(T - 2t')$, we have the points as represented

by the concentric circles. The curve through these points is an hyperbola whose equation is $P(T - 2t') = C = 240$.

This constant (240) is the average of 3,817 observations. We may, therefore, conclude that it requires an average accumulation of 240 effective day-degrees to bring the codling moth through the pupa stage. The observed variations from this average in the case of individuals were very great, due in some cases, no doubt, to errors in observation and in part to individual differences, but for the most part to the fact that the day was used as the unit of time. By using the day as the unit of time the actual period might in some cases be nearly a day shorter than the observed period, and in other cases nearly a day longer.

In midsummer the daily accumulation of effective day-degrees was sometimes as high as 27, so that the accumulation of day-degrees for some of the observed periods might be 27 day-degrees greater or less than for the actual period, or the average 240.

The following table shows the range of variations:

Number of individuals.	Day-degrees.
1	166
1	185-194
4	195-204
3	205-214
110	215-224
602	225-234
2238	235-244
653	244-255
170	254-265
18	264-275
7	274-285
7	284-295
2	294-305

Recorded accumulations of less than 205 or more than 275 were probably due to errors in observations; if we add 27 to the former and subtract 27 from the latter, we still have a variation of from 232 to 248 due to individual differences, humidity or other causes. The equation for the pupal period may, therefore, be written as follows:

$$P\ (T - 2t') = 240 \pm 8.$$

This paper was prepared merely to illustrate the method followed in determining the time-temperature factors, or the equation for the period. The method is applicable to the investigation of any stage of an insect.

If the threshold of development and the degree of the maximum rate of development should be found to be the same for each of

the stages of a given insect, the constant of the equation for the whole period from the deposition of the egg to the emergence of the adult may be found by adding the constants of the equations of the stages, and, by making suitable allowance for the time which elapses between the emergence of the adult and the deposition of eggs, a formula for the whole life cycle of the insect may be determined.

These equations may be of practical value in several ways.

By computing the normal daily effective day-degrees in any locality, the number of generations of the insect in that locality, and the normal dates on which the first eggs, or larvæ, may be expected to appear in that place can be ascertained. If any part of the season should be abnormally cold or warm, the amount of retardation or acceleration in development can be computed by keeping a daily record of the effective day-degrees and comparing them with the normal temperatures. In this way we should be able to ascertain when the injurious phase of any insect pest is approaching long enough beforehand to enable us to take whatever precautionary measures are necessary to avoid injury.

In the case of the codling moth, the dates when the larvæ of each generation may be expected to enter the fruit can be determined long enough beforehand to enable the owners to apply the spray at the right time.

How well this method of forecasting insect injuries will work out in practice only time can tell; however, the plan seems to be a feasible one, and one worth investigating.